Main prey and predators of Atlantic herring (*Clupea harengus* L.) in the Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

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Main prey and predators of Atlantic herring (*Clupea harengus* L.) in the Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

by

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ABSTRACT

Savenkoff, C., F. Grégoire, M. Castonguay, J.M. Hanson, D. Chabot, and D.P. Swain. 2006. Main prey and predators of Atlantic herring (*Clupea harengus* L.) in the Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2643: vi+28 pp.

We used results of mass-balance models to describe the changes in the structure and functioning of the northern and southern Gulf of St. Lawrence ecosystems related to the Atlantic herring populations (*Clupea harengus* L.) for the mid-1980s, the mid-1990s, and the early 2000s. Small and large zooplankton were the main prey of herring for each ecosystem and each time period. Herring was among the three main prey in both ecosystems for each time period. Predation was the main cause of herring mortality in the northern Gulf for all time periods and in the southern Gulf during the mid-1980s. Large cod (*Gadus morhua*) and redfish (*Sebastes* spp.) were progressively replaced by cetacea and seals as main herring predators from the mid-1980s to early 2000s in the northern Gulf. In the southern Gulf, large cod and harp seals were the main predators during the mid-1980s while predation and fishing mortality were of similar importance during the mid-1990s. Fishing was among the three main mortality causes in absolute terms in the northern and southern Gulf in each time period. Fishing effects on forage species since the early 1990s seem to counter the expected increases in biomass of these species following the net decrease in biomass of the demersal species and the ensuing drop in predation.

RÉSUMÉ

Savenkoff, C., F. Grégoire, M. Castonguay, J.M. Hanson, D. Chabot, and D.P. Swain. 2006. Main prey and predators of Atlantic herring (*Clupea harengus* L.) in the Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2643: vi+28 pp.

Nous avons utilisé les résultats de modèles d'équilibre de masse pour décrire les changements dans la structure et le fonctionnement des écosystèmes du nord et du sud du golfe du Saint-Laurent associés aux populations de hareng de l'Atlantique (*Clupea harengus* L.) pour le milieu des années 1980, le milieu des années 1990 et le début des années 2000. Le petit et le grand zooplancton étaient les principales proies du hareng dans chaque écosystème à chaque période de temps. Le hareng était parmi les trois principales proies dans les deux écosystèmes à chaque période de temps. La prédation était la principale cause de mortalité du hareng dans le nord du Golfe à chaque période de temps et dans le sud du Golfe pendant le milieu des années 1980. La grande morue (*Gadus morhua*) et le sébaste (*Sebastes* spp.) ont été progressivement remplacés par les cétacés et les phoques comme principaux prédateurs du hareng depuis le milieu des années 1980 jusqu'au début des années 2000 pour le nord du Golfe. Pour le sud du Golfe, la grande morue et le phoque du Groenland étaient les principaux prédateurs pendant le milieu des années 1980 alors que la prédation et la mortalité par pêche étaient d'égale importance pendant le milieu des années 1990. La mortalité par pêche était parmi les trois principales causes de mortalité en valeurs absolues dans le nord et le sud du Golfe à chaque période de temps. Les effets des pêches sur les espèces fourragères depuis le début des années 1990 semble masquer les augmentations attendues de biomasse de ces espèces suite à la diminution nette de la biomasse des espèces démersales et la chute résultante de leur prédation.

INTRODUCTION

In the northern and southern Gulf of St. Lawrence, ecosystem structure shifted dramatically from one previously dominated by piscivorous groundfish and small-bodied forage species (i.e., capelin [*Mallotus villosus*], mackerel [*Scomber scombrus*], herring [*Clupea harengus* L.], and shrimp [mostly northern shrimp, *Pandalus borealis*]) to one now dominated by small-bodied forage species and marine mammals (Savenkoff et al. 2004a and submitted a[1], b[2]). Overfishing removed a functional group, large piscivorous fish, which has not recovered ten years after the cessation of heavy fishing. This has left only marine mammals as top predators during the mid-1990s, although small Greenland halibut (*Reinhardtius hippoglossoides*) became important predators in the northern Gulf during the early 2000s. Overfishing during the 1980s appears to have caused a regime shift in the northern and southern Gulf ecosystems over the past two decades. These changes were accompanied by a decrease in total catches and a transition in landings from long-lived, piscivorous groundfish to planktivorous pelagic fish and invertebrates. Unfortunately, this trend in fishing down the food web is widespread in fisheries throughout the northern hemisphere (Pauly et al. 1998).

Shifts from ecosystems dominated by demersal fish to those dominated by pelagic fish (or short-lived species such as shrimp, crabs, or octopus) have been documented in the Atlantic and the Baltic (Worm and Myers 2003, Frank et al. 2005) and other coastal ecosystems (Jackson et al. 2001). Large piscivorous groundfish predators declined dramatically, but their prey (herring, capelin, shrimp, and snow crab) increased in abundance (Lilly 1991, Berenboim et al. 2000, Garrison and Link 2000, Koeller 2000, Lilly et al. 2000). With capelin and Atlantic mackerel, Atlantic herring comprised a large pelagic forage base that supported the high level of predation in the Gulf of St. Lawrence when large piscivorous groundfish were still abundant (i.e., mid-1980s; Savenkoff et al. 2004a). Subsequent research survey data revealed a major expansion in the geographical distribution of capelin throughout the Gulf of St. Lawrence in the 1990s (DFO 2001, Savenkoff et al. 2004b). In contrast, the biomass of Atlantic mackerel, a partially piscivorous forage fish species, decreased from the mid-1980s to early 2000s in the northern Gulf (from 2.46 ± 0.85 to 0.52 ± 0.29 t km^{-2}) and from the mid-1980s to mid-1990s in the southern Gulf (from 4.93 ± 1.70 to 1.16 ± 0.90 t km^{-2}) (Savenkoff et al. 2005a). These authors also showed that fishing mortality of mackerel increased and became the most important cause of mortality in the northern Gulf for the early 2000s and the principal cause of mortality in the southern Gulf for the mid-1990s. Based on the results of mass-balance models, this report examined the changes in the structure and functioning of the northern and southern Gulf of St. Lawrence ecosystems for the mid-1980s, the mid-1990s, and the early 2000s with respect to the Atlantic herring populations. Our results enabled us to evaluate the main prey and predators of herring as well as the effects of fishing and predation on this species for both ecosystems and each time period.

[1]: Savenkoff, C., Castonguay, M., Chabot, D., Bourdages, H., Morissette, L., and Hammill, M. O. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? Submitted for publication.

[2]: Savenkoff, C., Swain, D. P., Hanson, J. M., Castonguay, M., Hammill, M. O., Bourdages, H., Morissette, L., and Chabot, D. Effects of fishing and predation in a heavily exploited ecosystem: Comparing pre- and post-groundfish collapse periods in the southern Gulf of St. Lawrence (Canada). Submitted for publication.

MATERIAL AND METHODS

Data used in modelling

The study area in the northern Gulf of St. Lawrence (Northwest Atlantic Fishing Organization [NAFO] divisions 4RS) covers an area of 103,812 km^2 (Figure 1). The nearshore region (depths < 37 m) was not included in the models. In NAFO division 4T (southern Gulf), our study area was defined as the region with depths between 15 and 200 m, covering an area of 64,075 km^2, which excluded the deep parts of the Laurentian Channel (survey strata 415, 425, and 439) and the St. Lawrence Estuary (Figure 1). In both study areas, the shallower zone was excluded from the models because it is not covered by annual summer bottom-trawl surveys and because exchanges between the infra-littoral and mid- to off-shore zones are still poorly understood. American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) were not included in the models. The periods covered by this analysis are the pre-collapse (mid-1980s: 1985–1987) and post-collapse (mid-1990s: 1994–1996) periods of groundfish stocks in both areas. For the northern Gulf, another period was also studied: the early 2000s (2000–2002), a few years after a limited cod (*Gadus morhua*) fishery had resumed in the northern Gulf.

Based on data availability and the ecological and commercial significance of the species, the organisms inhabiting the northern Gulf of St. Lawrence were divided into selected functional groups or compartments (32 for the mid-1980s and mid-1990s, 31 for the early 2000s) (Table 1). The model structure for the early 2000s differs slightly from that used for the mid-1980s and mid-1990s for the following reasons: (1) improved knowledge: cetaceans were separated into mysticeti (baleen whales) and odontoceti (toothed whales); (2) newly acquired data on the biomass of shrimp and crab size classes that allowed us to separate these species into small and large groups for the early 2000s; (3) very low species biomass for the early 2000s: sand lance *Ammodytes* spp. were included in the planktivorous small pelagic feeders group for the early 2000s (biomass: 0.003 t km^{-2} vs 2.398 and 0.120 t km^{-2} for the mid-1980s and mid-1990s, respectively); and (4) a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for hooded seals (*Cystophora cristata*), harbour seals (*Phoca vitulina*), and Arctic cod (*Boreogadus saida*) resulted in these groups being combined with the harp seal (*Pagophilus groenlandicus*), grey seal (*Halichoerus grypus*), and capelin groups, respectively, for the early 2000s. For the mid-1980s and mid-1990s, we distinguished five marine mammal groups, one seabird group, sixteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group. For the early 2000s, we distinguished four marine mammal groups, one seabird group, fourteen fish groups, ten invertebrate groups, one phytoplankton group, and one detritus group. Shrimp and crabs were each separated into two groups. Based on an average size at sex change (22 mm carapace length, CL), shrimp were separated into large shrimp (≥ 22 mm CL), mainly female *Pandalus borealis*, which are recruited to the fishery, and small shrimp (< 22 mm CL), mainly male *P. borealis* and individuals from other shrimp species, which are partially recruited to the fishery (DFO 2002). Based on important differences in diet, vulnerability to predation (in particular cannibalism; crab prey ranged between 3.9 and 48.8 mm carapace width, CW), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) crabs (Lovrich and Sainte-Marie 1997). Only the large crab group is recruited to the fishery, and catches consist exclusively of male snow crab, *Chionoecetes opilio*.

In the southern Gulf of St. Lawrence, we distinguished 30 functional groups consisting of five marine mammal groups, one seabird group, fourteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group for the mid-1980s and mid-1990s (Table 1). No model was constructed for the early 2000s.

In both ecosystems, some groups, such as large pelagic and demersal feeders, are composite groups, where the species were aggregated based on similarity in size and ecological role. Atlantic cod, Greenland halibut (in the northern Gulf), and American plaice (*Hippoglossoides platessoides*) (in the southern Gulf) were, for some models, separated into two groups based on diet, minimum age/size at capture, and age/size at maturity. Juveniles of these species prey mainly on invertebrates while larger individuals feed mostly on fish. These changes tend to occur gradually with increasing length, but for these models it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and American plaice (Pitt 1973) and at 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of length-frequency data and information on diet compositions of small versus large fish as well as on the proportions of juvenile and adult fish in the diets of their predators, we could not distinguish juveniles and adults for other fish species.

To estimate the magnitude of trophic fluxes, the models require measurements or estimates of different parameters (input data) such as population biomass, diet composition, and landings as well as consumption and production rates for different living compartments. For the northern Gulf, diet composition and other input data (biomass, production, consumption, and export) for each compartment as well as calculation details are described in Morissette et al. (2003) for the mid-1980s, Savenkoff et al. (2004c) for the mid-1990s, and Savenkoff et al. (2005b) for the early 2000s. For the southern Gulf, further details on the calculation of diet composition and the other input data (biomass, production, consumption, and export) for each compartment are given in Savenkoff et al. (2004d). These four technical reports are available online: www.osl.gc.ca/cdeena/en/publications.shtml.

Inverse modelling

Inverse models use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy between components of an ecosystem and to generate a "snapshot" of the system at one moment in time (Vézina and Platt 1988; Savenkoff et al. 2004a). As opposed to traditional approaches, the ecosystem is considered as a whole, taking into account trophic interactions between all functional groups. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data, straightforward mass balance, and metabolic constraints.

In inverse modelling, we assumed that there was no change in biomass during each studied time period and that net migration was zero (migration out of or into the study area, food intake of predators that are not part of the system, etc.). Under this steady-state assumption, the sum of inflows (consumption for each consumer group) is balanced by the sum of outflows (production, respiration, and egestion for each consumer group). Also, production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed other mortality causes or MO). Other mortality causes could include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004a), unsuspected migration, or other processes not accounted for

in the model. For phytoplankton, the net production (corrected for respiration) must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (2004a and submitted a, b).

The models are useful in constraining observations into coherent pictures (Savenkoff et al. 2004a and submitted a, b); however, since the number of flows to be solved exceeded the number of independent mass balance relations (i.e., an underdetermined system), there is no unique solution to any model. Also, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other valid solutions are possible. However, for each model presented in the next section, the final solution is always the mean of 30 iterations with random perturbations of the input data (to a maximum of their standard deviations) and one solution without perturbation (the "initial solution") to provide an overall view of the ecosystem and to identify robust patterns. The estimated flows fell inside our *a priori* constraints and therefore were a reasonable "middle ground" description. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003).

Background on herring

Herring is a pelagic species that forms large schools during feeding, spawning, and migration periods (DFO 2003). Eggs are attached to the bottom, and large females produce more eggs than small females. First spawning occurs primarily at age four.

The herring population in the northeast Gulf (4R) consists of two stocks, one spawning in spring and one in the fall, with July 1st as the separation date for their spawning seasons. Spring spawners generally lay their eggs in May and April, while egg laying of fall spawners occurs in August and September. Historically, the spring-spawning stock congregates off the west coast of Newfoundland and in and around St. George's Bay (McQuinn et al. 1999). Over the past few years, however, there have been growing indications that other spawning grounds exist in the large bays farther north. The fall-spawning stock regroups further up the coast, north of Point Riche, from mid-July to mid-September to reproduce (McQuinn et al. 1999). Outside the spawning season, these two stocks are found mainly in St. George's Bay in the spring, north of Point Riche and in the Strait of Belle Isle in the summer, and off Bonne Bay in the fall (McQuinn et al. 1999). Winter survey catches in the northern Gulf of St. Lawrence in the 1980s and the early 1990s indicated that the herring over-winter in the deep waters of the Esquiman Channel. The herring stocks are harvested separately as spawning aggregations and collectively when the stocks are mixed (DFO 2003). Very little information was available for herring in 4S. The presence of the same strong year-classes (1987–1989) in (1) the inshore gillnet fishery of the eastern part of NAFO division 4S (Québec lower north shore), (2) Esquiman Channel during the fall and winter research surveys, and (3) the late-fall purse seine fishery of the west coast of Newfoundland suggests that local spawners from Québec's lower north shore could migrate to 4R in the fall (McQuinn and Lefebvre 1995).

Herring in the southern Gulf of St. Lawrence is found in the area extending from the north shore of the Gaspé Peninsula to the northern tip of Cape Breton Island, including the Îles-de-la-Madeleine. Adults overwinter off the north and east coast of Cape Breton in NAFO areas 4T and 4Vn (Claytor 2001, Simon and Stobo 1983). The herring population in the southern Gulf also consists of two spawning components. Spring spawning occurs primarily in April-May but extends into June at depths <10 m. Fall spawning occurs from mid-August to mid-October at depths of 5 to 20 m. The largest spring spawning beds are in Northumberland Strait and around the Îles-de-la-Madeleine. The largest fall spawning beds are on the Miscou and Escuminac (New Brunswick), Tignish and Fisherman's (Prince Edouard Island), and Pictou (Nova Scotia) banks (LeBlanc et al. 2005). Herring in the southern Gulf is harvested primarily by an inshore gillnet fleet (fixed gear) and a smaller purse seine fleet (mobile gear), both fishing in NAFO area 4T and, in some years, 4Vn (LeBlanc et al. 2005). The inshore fleet harvests almost solely the spring spawner component in the spring and almost solely the fall spawner component in the fall. The purse-seine fleet harvests a mixture of spring and fall spawners, both in the spring fishery, which occurs in the area between Cape Breton Island and the Îles-de-la-Madeleine, and the fall fishery, which takes place in Chaleur Bay, north of P.E.I., and off western Cape Breton. Since 1981, the inshore fixed-gear fleet has accounted for most of the catch of spring and fall spawners (LeBlanc et al. 2005).

Input data (biomass, production, consumption, and catch) used in modelling and estimated fluxes for herring for both ecosystems (4RS and 4T) and each period are summarized in Table 2. Several scenarios were tested for 1985–1987 in the northern Gulf. Here, we used the estimates from the most realistic solution, the "misreporting solution" that included misreported catches of large cod (Savenkoff et al. 2004a). In this solution, the catches of large cod have been increased by 30%, a level consistent with estimates of misreported cod catches in the northern Gulf in the mid-1980s (Fréchet 1991, Palmer and Sinclair 1997).

In our northern and southern Gulf models, the planktivorous small pelagic feeders group includes herring, Atlantic argentine (*Argentina silus*), planktivorous myctophids, sand lance (northern sand lance *Ammodytes dubius*, and American sand lance *A. americanus*), and other mesopelagics (rainbow smelt, alewife, etc.). Herring was the most important in terms of biomass (at least 70% of the group's biomass) and was therefore considered the key species for the group. Some input values and modelling estimates were slightly different from data published in previous technical reports (Morissette et al. 2003, Savenkoff et al. 2004c, d, Savenkoff et al. 2005b) due to model updates.

Catch

In the northern Gulf, herring was the only species of the planktivorous small pelagic feeders group for which catch statistics were available. Commercial landings were estimated from NAFO landing statistics (NAFO 2003). In the northern Gulf, the mean annual catch was 18,312 t or 0.18 t km^{-2} yr^{-1} (SD: 0.03 t km^{-2} yr^{-1}; range: 0.14-0.21 t km^{-2} yr^{-1}) during the 1985–1987 period, 14,893 t or 0.14 t km^{-2} yr^{-1} (SD: 0.03 t km^{-2} yr^{-1}; range: 0.12-0.16 t km^{-2} yr^{-1}) during the 1994–1996 period, and 12,978 t or 0.13 t km^{-2} yr^{-1} (SD: 0.01 t km^{-2} yr^{-1}; range: 0.12-0.13 t km^{-2} yr^{-1}) during the 2000–2002 period (Table 2). On average, landings in 4R accounted for 97% of the total catches in 4RS. Catches estimated by the models were 0.18, 0.15, and 0.13 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively (Table 2).

In the southern Gulf, the landings for the planktivorous small pelagic feeders group were also calculated by summing NAFO landing statistics for each of the species listed above (NAFO 2003). For Atlantic herring, the mean annual landings in 4T were 58,361 and 82,990 t during the 1985–1987 and 1994–1996 periods, respectively. For rainbow smelt, the mean annual landings in 4T were 1,609 and 1,106 t during the 1985–1987 and 1994–1996 periods, respectively. For alewife, the mean annual landings in 4T were 5,233 and 3,266 t during the 1985–1987 and 1994–1996 periods, respectively. This resulted in mean annual catches of planktivorous small pelagics of 1.02 ± 0.32 and 1.36 ± 0.12 t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively (Table 2). Catches of planktivorous small pelagics estimated by the models were 0.95 and 1.35 t km^{-2} yr^{-1}, respectively, for each period (Table 2).

Biomass

In the northern Gulf, the average biomass of herring (the key species for the planktivorous small pelagic feeders group) in the eastern part of the study area (NAFO zone 4R) was taken from the sequential population analysis (SPA) by McQuinn et al. (1999) for the 1985–1987 and 1994–1996 periods and by Grégoire et al. (2004a, b) for the 2000–2002 period. Data for herring populations in 4S were unavailable. However, based on newly acquired data and fishery observations (the presence of large fish and strong year-classes that have been observed in the gillnet fishery for many years; bays with milky white opaque and creamy water from enormous spawn), we thought that it was better to attempt, to the best of our ability, to estimate the 4S biomass than to ignore it. Thus, based on 4R biomass values estimated by SPA and the ratios of catch rates in 4S to catch rates in 4R of the annual summer bottom-trawl surveys, we estimated the biomass in 4S for each period. The herring biomass was 304,084 t or 2.93 t km^{-2}, 117,924 t or 1.14 t km^{-2}, and 369,935 t or 3.56 t km^{-2} during the 1985–1987, 1994–1996, and 2000–2002 periods, respectively. Biomass in 4S accounted for 16% of the total biomass in 4RS during the mid-1980s (12% during the mid-1990s), while it represented 63% of the total biomass during the early 2000s. The biomass of Atlantic argentine and planktivorous myctophids in the study area, which was estimated from annual summer bottom-trawl surveys, was 8,100 t or 0.08 t km^{-2}, 1,318 t or 0.01 t km^{-2}, and 894 t or 0.009 t km^{-2} during the 1985–1987, 1994–1996, and 2000–2002 periods, respectively. Total biomass for the planktivorous small pelagic feeders group was 3.01 t km^{-2} (SD: 0.11 t km^{-2}), 1.15 t km^{-2} (SD: 0.14 t km^{-2}), and 3.57 t km^{-2} (SD: 1.90 t km^{-2}) during the 1985–1987, 1994–1996, and 2000–2002 periods, respectively (Table 2).

In the southern Gulf, the average biomass of herring was taken from SPA (LeBlanc et al. 2001). The spring and autumn spawner biomasses were used in the estimate (ages 2 and older). The biomasses for other species were estimated from the annual summer bottom-trawl surveys and corrected for catchability. The mean biomass estimates for planktivorous small pelagics were 625,027 t or 9.76 t km^{-2} (SD: 1.82 t km^{-2}) and 475,513 t or 7.42 t km^{-2} (SD: 0.15 t km^{-2}) during the mid-1980s and mid-1990s, respectively (Table 2).

Production

In the northern Gulf, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality was set to 0.2 yr^{-1} (McQuinn

et al. 1999). When the minimum and maximum biomass values were used for each period, we obtained production ranges of 0.71 to 0.75 t km^{-2} yr^{-1} (mean: 0.73 ± 0.02 t km^{-2} yr^{-1}) for 1985–1987, 0.35 to 0.38 t km^{-2} yr^{-1} (mean: 0.37 ± 0.02 t km^{-2} yr^{-1}) for 1994–1996, and 0.59 to 1.27 t km^{-2} yr^{-1} (mean: 0.84 ± 0.37 t km^{-2} yr^{-1}) for 2000–2002 (Table 2). Herring productions estimated by the models were 0.74, 0.38, and 1.22 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively (Table 2).

In the southern Gulf, natural mortality was also assumed to be 0.2 yr^{-1} for herring (LeBlanc et al. 2001). An M value of 0.44 yr^{-1} was estimated for rainbow smelt and alewife using FishBase (Froese and Pauly 2002). When the minimum and maximum biomass values were used for each period, we obtained a production range of 2.71 to 3.92 (mean: 3.21 ± 0.64 t km^{-2} yr^{-1}) and 2.79 to 3.12 t km^{-2} yr^{-1} (mean: 2.95 ± 0.10 t km^{-2} yr^{-1}), respectively, for 1985–1987 and 1994–1996 (Table 2). Model estimates were 3.38 t km^{-2} yr^{-1} and 3.06 t km^{-2} yr^{-1} during the mid-1980s and mid-1990s, respectively (Table 2).

Consumption

Consumption (Q) of planktivorous small pelagics was estimated by multiplying biomass (B) by the Q/B ratios derived from the literature. During summer, consumption rates of herring in the Baltic Sea were estimated to vary from 10 to 20% of body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups (Rudstam et al. 1992). During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1}. Values taken from Pauly (1989) were 4.590 yr^{-1} for fish from Georges Bank and 10.100 yr^{-1} for fish from the North Sea. Finally, Fetter and Davidjuka (1996) estimated daily food consumption for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual Q/B of 2.798 yr^{-1}.

In the northern Gulf, when the minimum and maximum biomass values and these different Q/B ratios were used, we obtained a consumption range of 8.09 to 42.52 t km^{-2} yr^{-1} for 1985–1987, 2.86 to 17.88 t km^{-2} yr^{-1} for 1994–1996, and 6.44 to 78.69 t km^{-2} yr^{-1} for 2000–2002. Based on the mean production for each period and the minimum and maximum gross growth efficiency limits (GE: the ratio of production to consumption, 10–30%; Christensen and Pauly 1992), we obtained consumption values of 2.45 and 7.35 t km^{-2} yr^{-1} for 1985–1987, 1.24 and 3.73 t km^{-2} yr^{-1} for 1994–1996, and 2.80 and 8.39 t km^{-2} yr^{-1} for 2000–2002. The resulting lower and upper consumption limits used were 2.45 and 42.52 t km^{-2} yr^{-1} for 1985–1987, 1.24 and 17.88 t km^{-2} yr^{-1} for 1994–1996, and 2.80 and 78.69 t km^{-2} yr^{-1} for 2000–2002 (Table 2). The inverse solution estimated a consumption of 2.57 t km^{-2} yr^{-1} for 1985–1987, 2.27 t km^{-2} yr^{-1} for 1994–1996, and 7.11 t km^{-2} yr^{-1} for 2000–2002 in the northern Gulf (Table 2).

In the southern Gulf, when the minimum and maximum biomass values for each period and the Q/B ratios from the literature were used, we obtained consumption ranges of 24.02 to 162.15 t km^{-2} yr^{-1} for 1985–1987 and 20.39 to 103.84 t km^{-2} yr^{-1} for 1994–1996. Based on the mean production for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 10.72 to 32.15 and 9.82 to 29.46 t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively. The resulting lower and upper consumption limits used were 10.72 to 162.15 t km^{-2} yr^{-1} and 9.82 to 103.84 t km^{-2} yr^{-1}, respectively, for the two periods (Table 2). The

inverse solution estimated a consumption of 19.54 and 20.09 t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively (Table 2).

Diet composition

For 1985–1987 in the northern Gulf, we used the diet composition of the planktivorous small pelagics estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and the stomach content data available from NAFO zone 4T (M. Hanson, unpublished data) (Table 3). The study of Darbyson et al. (2003) was also included for 1994–1996 and 2000–2002 (Table 3). For each time period, we decided to use all the available diet compositions, even though they were from the southern Gulf.

In the southern Gulf, diet composition was derived from two sources of information on planktivorous small pelagics. Stomach content data for herring were available from NAFO division 4T from April to September 1999 (n = 718) (M. Hanson, unpublished data). We used these diet data for the two periods. However, for the mid-1980s, we also used the diet composition estimated for the Newfoundland–Labrador Shelf (Bundy et al. 2000). When the southern models were completed, the study of Darbyson et al. (2003) was not available. The resulting diet composition is shown in Table 4.

RESULTS

Main prey groups consumed by herring

In the northern Gulf, small and large zooplankton were the main prey for each time period (Figure 2). In our models, large zooplankton are organisms and species greater than 5 mm in length and include euphausiids (mainly *Thysanoessa raschii, T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula, Parathemisto abyssorum*, and *P. gaudichaudii*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis arctica*), tunicates, and ichthyoplankton. The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus, C. hyperboreus*, and *Oithona similis*, are the most numerous species of small zooplankton (Roy et al. 2000). In our inverse models, we were not able to estimate the individual proportion of each species aggregated in large and small zooplankton groups consumed by herring. Small and large zooplankton accounted for 82 and 11% of the diet during the mid-1980s and 73 and 16% of the diet during the early 2000s, while the pattern is reversed during the mid-1990s (29 and 61% of the diet). However, as shown by the standard deviation, the differences were not statistically significant. Other herring prey were benthic invertebrates (between 7 and 10% of the diet for each time period). The overall consumption of herring was similar for the mid-1980s and mid-1990s (close to 2.5 t km^{-2} yr^{-1}) while it increased by a factor of three during the early 2000s (7.1 t km^{-2} yr^{-1}).

In the southern Gulf, small and large zooplankton were the most important prey for the mid-1980s and mid-1990s (94 and 99% of the diet) (Figure 3). During the mid-1980s, other benthic invertebrates contributed 6% of the diet. The overall consumption of herring was similar for each time period (close to 20 t km^{-2} yr^{-1}).

Role played by herring in the northern and southern Gulf ecosystems

Herring were among the main prey groups in the two Gulf ecosystems. In the northern Gulf, when planktonic and benthic invertebrate groups were not considered in the calculation, capelin was the major prey in the system (between 57 and 63% of matter consumed; Figure 4). The other main prey groups were planktivorous small pelagics (e.g., herring and sand lance), redfish (*Sebastes* spp.), and shrimp during the mid-1980s while shrimp and planktivorous small pelagics were heavily consumed during the mid-1990s. There was a four-fold decrease in the matter consumed from the mid-1980s to mid-1990s (from 19.1 ± 3.0 to 4.8 ± 0.5 t km^{-2} yr^{-1}). From the mid-1990s to the early 2000s, there was an increase in the amount of matter consumed within the ecosystem (from 4.8 ± 0.5 to 7.3 ± 0.9 t km^{-2} yr^{-1}). The main prey was capelin (43% of matter consumed), followed by shrimp (22%) and planktivorous small pelagics (14%). Herring was consumed by between 17 and 19 predators and was among the three main prey in the northern Gulf at each time period.

In the southern Gulf, there was no difference in the amount of matter consumed within the ecosystem from the mid-1980s to the mid-1990s (8.1 t km^{-2} yr^{-1}; Figure 5) when planktonic and benthic invertebrate groups were not considered in the calculations. However, the relative size of the compartments processing this matter changed substantially. Planktivorous small pelagics, shrimp, small American plaice, and piscivorous small pelagics (mainly mackerel) were the main prey in the southern Gulf (combined = 65% of matter consumed) during the mid-1980s (Figure 5). In contrast, capelin was the most important prey during the 1990s, followed by shrimp, planktivorous small pelagics, and small American plaice (combined = 79% of matter consumed). Herring was consumed by 17 predators in each time period.

Main causes of herring mortality

In the northern Gulf, predation was the main cause of herring mortality during the mid-1980s (69% of total mortality) while fishing and other mortality causes represented 24 and 8% of total mortality, respectively (Figure 6). Redfish was the main predator (24% of the total mortality), followed by fishing (24%) and large cod (20%). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.20, 0.07, and 0.02 yr^{-1}, respectively (total: 0.29 yr^{-1}). From the mid-1980s to mid-1990s, there was a decrease in total mortality from 0.74 ± 0.15 to 0.38 ± 0.04 t km^{-2} yr^{-1}. Also, predation decreased from 0.51 ± 0.14 to 0.22 ± 0.04 t km^{-2} yr^{-1} during the same time period. Predation dominated total mortality (57% of total mortality) during the mid-1990s while fishing and other mortality causes accounted for 38 and 5%, respectively. During the mid-1990s, cetacea and large Greenland halibut (32 and 9% of total mortality, respectively) were the main predators of herring (Figure 6). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.19, 0.13, and 0.02 yr^{-1}, respectively (total: 0.33 yr^{-1}). From the mid-1990s to the early 2000s, total mortality values increased from 0.38 ± 0.04 to 1.22 ± 0.30 t km^{-2} yr^{-1}. Also, predation increased from 0.22 ± 0.04 to 1.03 ± 0.30 t km^{-2} yr^{-1} during the same time period. Predation dominated total mortality (85% of total mortality) during the early 2000s, while fishing and other mortality causes accounted for 10 and 5%, respectively. Harp seals, cetacea, and large cod were the main predators (20, 18, and

10% of total mortality, respectively) (Figure 6). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.29, 0.04, and 0.02 yr^{-1}, respectively (total: 0.34 yr^{-1}).

In the southern Gulf, predation was also the main cause of herring mortality during the mid-1980s (65% of total mortality; Figure 7). Fishing and other mortality causes represented 28 and 7% of total mortality, respectively. Large cod were the main predators, followed by harp seals (22 and 11% of total mortality, respectively). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.22, 0.10, and 0.03 yr^{-1}, respectively (total: 0.35 yr^{-1}). From the mid-1980s to mid-1990s, total mortality values were similar (3.38 ± 0.43 t km^{-2} yr^{-1} vs 3.06 ± 0.53 t km^{-2} yr^{-1}; Figure 7). However, predation decreased from 2.18 ± 0.37 to 1.28 ± 0.41 t km^{-2} yr^{-1} during the same time period while fishing increased from 0.95 ± 0.12 to 1.35 ± 0.07 t km^{-2} yr^{-1}. Predation and fishing mortality were of similar importance (nearly 43% of total mortality) during the mid-1990s while other mortality causes accounted for 14%. Large cod and large demersals were the main predators (8 and 7% of total mortality, respectively; Figure 7). In absolute terms, fishing mortality was still the main mortality cause. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.17, 0.18, and 0.06 yr^{-1}, respectively (total: 0.41 yr^{-1}).

DISCUSSION / CONCLUSION

In the northern and southern Gulf of St. Lawrence, exploitation influenced community structure directly through preferential removal of larger-bodied fishes and indirectly because larger-bodied fishes exerted top-down control upon other community species or competed with other species for the same prey. The net decrease in biomass of the demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to ecosystem structures dominated by small-bodied pelagic species and marine mammals in the northern and southern Gulf. This has left marine mammals as top predators in the northern Gulf during the mid-1990s and marine mammals and small Greenland halibut during the early 2000s (Savenkoff et al. submitted a). In the southern Gulf, although the impact of seals also increased during the mid-1990s, large cod remained one of the most important predators on fish, though the combined predation by harp and grey seals did exceed predation by large cod (Savenkoff et al. submitted b).

In the southern Gulf, the models indicated that predation decreased mainly from the mid-1980s to mid-1990s. Predation was the main cause of herring mortality in the southern Gulf during the mid-1980s while predation and fishing mortality were of similar importance during the mid-1990s. Fishing mortality increased from the mid-1980s to mid-1990s in the southern Gulf. This pattern was similar to the impact of fishing mortality on mackerel found by Savenkoff et al. (2005a). Indeed, fishing mortality on mackerel increased and became the second cause of mortality in the northern Gulf for the early 2000s and the main cause of mortality in the southern Gulf for the mid-1990s. This is related to the net transition in landings from long-lived, piscivorous groundfish in the 1980s toward small-bodied, planktivorous pelagic fish and a variety of invertebrates since the early 1990s. Increased fishing mortality may have countered the expected increase in biomass of forage species following the net decrease in demersal-fish biomass and the ensuing drop in predation.

In the northern Gulf ecosystem, the models indicated that predation was the main cause of herring mortality for all time periods. There was a net decrease in total mortality and predation

on herring from the mid-1980s to mid-1990s. From the mid-1990s to early 2000s, both total mortality and predation increased in the northern Gulf. Fishing mortality decreased over the three time periods. However, fishing was among the three main mortality causes in absolute terms in the northern Gulf in each time period. Specifically, the biomass of herring decreased from the mid-1980s to the early 2000s in the 4R area (from 254,971 t to 118,825 t) while biomass increased in 4S (from 49,113 t to 251,110 t). Catches decreased in the two areas from the mid-1980s to the early 2000s (4R: from 17,461 t to 13,086 t; 4S: from 851 t to 221 t). Thus, herring biomass increased following the net decrease in biomass of the demersal species and the ensuing drop in predation in 4S, where the fishing effect was weak. In 4R, increased fishing mortality on herring also seemed to counter the expected increases in biomass of these species. However, biomass in 4S, which was based on catch rates from the research vessel bottom trawl survey, was a crude estimate. There is little information available for the 4S herring populations and for exchanges between 4S and 4R herring populations. Also, as far as we know, there is currently little mixing of the northern and southern populations.

Monitoring programs (fishery statistics, commercial sampling, and research surveys) allow a fair assessment of the past and current status of the stocks. Ecosystem models could become powerful new tools for fishery management. The model results already provide valuable information on the impact of fishing effort and catch rates of the exploited species in the northern and southern Gulf and on the effects of the major mortality causes (fishing, predation, and natural mortality other than predation) on the fish and invertebrate communities.

Modelling of large marine ecosystems is still in its infancy. Our current models, even with 30 compartments, still represent simplifications of the trophic interactions in the northern and southern Gulf of St. Lawrence. The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence that we have in them). This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence at three time periods and in the southern Gulf at two time periods. Here, the models produced values that were logically consistent with our model structure and constraints. These values were meaningful in the sense that they met some clearly imposed constraints that reflect how we think the system is working. However, even though the model was useful in constraining observations into a coherent picture, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other equivalent solutions are possible. The model is able to derive logical solutions that narrow the range of possibilities. Several configurations were rejected, e.g. model solutions that included possible parameter values incompatible with the model constraints based on the ranges of input data. Also, the random perturbations showed that the ecosystem configuration that minimized least-square errors was robust, even with strong perturbations in the input data (Savenkoff et al. 2004a and submitted a, b). However, even though most of the data are good estimates for the 4RS and 4T ecosystems, some input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. The uncertainties remaining in the understanding of the ecosystem may come from (i) incorrect values because no data exist, (ii) the confidence limits being too large, (iii) an inaccurate aggregation of species within one functional group, or (iv) unknown mechanisms. Overall, even though the model is not a perfect representation of reality, it is probably as good as it can be with the information available. Such a model provides a useful starting point to frame

hypotheses about the ecosystem, to identify data gaps, and to show where the uncertainties in the food web occur, that could be examined in future studies. Progress is still needed to refine our understanding of the structure of ecosystems and to enhance the quality of future modelling efforts in the Gulf of St. Lawrence as well as in other areas of the world. Information on the impact of fishing and predation on the Atlantic herring stocks in the Gulf of St. Lawrence has to continue to be collected to adapt management strategies to the current predator and prey stock situation and to ensure that the biomass of one of the most important forage species remains at a level that meets the predator needs in the future.

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See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

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Table 1. Functional groups used in modelling in the northern and southern Gulf of St. Lawrence for each time period.

Group name	Main species
Cetaceans[a]	Mysticeti or baleen whales: *Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*
	Odontoceti or toothed whales: *Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals[b]	*Pagophilus groenlandicus*
Hooded seals[b]	*Cystophora cristata*
Grey seals[c]	*Halichoerus grypus*
Harbour seals[c]	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delawarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)[d]	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)[d]	*Reinhardtius hippoglossoides*
Large American plaice (> 35 cm)[e]	*Hippoglossoides platessoides*
Small American plaice (≤ 35 cm)[e]	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[f]	*Ammodytes* spp.
Arctic cod[g]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp[h]	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Eualus macilentus*, *E. gaimardii*
Crabs[i]	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Strongylocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogone hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiosira nordenskioeldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Cetaceans were separated into two groups for the early 2000s in the northern Gulf model: the mysticeti (baleen whales) and the odontoceti (toothed whales).

[b]: Harp and hooded seals were grouped for the northern Gulf model in the early 2000s.

[c]: Grey and harbour seals were grouped for the northern Gulf model in the early 2000s.

[d]: Aggregated as Greenland halibut for the southern Gulf models.

[e]: Aggregated as American plaice for the northern Gulf models.

[f]: Included in the planktivorous small pelagic feeders for the southern Gulf models and for the northern Gulf model in the early 2000s.

[g]: Included in the capelin group for the southern Gulf models and for the northern Gulf model in the early 2000s.

[h] Shrimp were separated into large shrimp, mainly females (≥ 22 mm CL; mainly *Pandalus borealis*), and small shrimp (< 22 mm CL) for the northern Gulf model in the early 2000s.

[i]: Crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) crabs for the northern Gulf model in the early 2000s.

Table 2. Observed mean, minimum, and maximum values for herring made using inverse modelling for each ecosystem and each time period. Modelling estimates are also shown. Inverse modelling does not estimate biomass. Values used in data equations or as upper and lower limit constraints are indicated in boldface[a].

Parameter	Northern Gulf			Southern Gulf	
	1985–1987	1994–1996	2000–2002	1985–1987	1994–1996
Mean catch (t km^{-2} yr^{-1})	**0.18**	**0.14**	**0.13**	**1.02**	**1.36**
Minimum catch (t km^{-2} yr^{-1})	0.14	0.12	0.12	0.70	1.23
Maximum catch (t km^{-2} yr^{-1})	0.21	0.16	0.13	1.33	1.46
Estimated catch (t km^{-2} yr^{-1})	0.18	0.15	0.13	0.95	1.35
Mean biomass (t km^{-2})	3.01[b]	1.15[b]	3.57	9.76	7.42
Minimum biomass (t km^{-2})	2.89[b]	1.02[b]	2.30	8.58	7.29
Maximum biomass (t km^{-2})	3.11[b]	1.31[b]	5.75	11.85	7.59
Mean production (t km^{-2} yr^{-1})	0.73	0.37	0.84	3.21	2.95
Minimum production (t km^{-2} yr^{-1})	**0.71**	**0.35**	**0.59**	**2.71**	**2.79**
Maximum production (t km^{-2} yr^{-1})	**0.75**	**0.38**	**1.27**	**3.92**	**3.12**
Estimated production (t km^{-2} yr^{-1})	0.74	0.38	1.22	3.38	3.06
Mean consumption (t km^{-2} yr^{-1})	22.49	9.56	40.74	86.43	56.83
Minimum consumption (t km^{-2} yr^{-1})	**2.45**	**1.24**	**2.80**	**10.72**	**9.82**
Maximum consumption (t km^{-2} yr^{-1})	**42.52**	**17.88**	**78.69**	**162.15**	**103.84**
Estimated consumption (t km^{-2} yr^{-1})	2.57	2.27	7.11	19.54	20.09

[a]: Some of the input data were introduced directly into the models as data equations. The data equations attempt to fix the value of certain flows or combinations of flows. These included mean values (e.g., catch) estimated from field studies and values available only as point estimates (no variance) or with low observed values (e.g., <0.5%) and low uncertainty (e.g., SD < 0.6%). The production and consumption values that were not estimated from local field studies as well as the diet proportions with higher values (e.g., >0.5%) were incorporated as constraints.

[b]: These values do not include the biomass of sand lance. During the early 2000s, planktivorous small pelagics and sand lance were aggregated, but the biomass of sand lance was very low (0.2% of total biomass).

Table 3. Diet composition of herring used in modelling of the northern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Northern Gulf	1985–1987					1994–1996 and 2000–2002				1994–1996	2000–2002
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est	Est
Small cod						**0.0**	0.0	0.0	0.0	0.0	0.0
American plaice						**0.0**	0.0	0.0	0.0	0.0	0.0
Flounders						**0.0**	0.0	0.0	0.0	0.0	0.0
Small demersals						**0.0**	0.0	0.0	0.0	0.0	0.0
Capelin						1.9	2.9	**0.0**	**4.1**	0.3	0.3
Pisci. small pelagics						0.5	0.0	**0.0**	**0.5**	0.0	0.5
Plank. small pelagics						**0.1**	0.2	0.0	0.3	0.1	0.1
Shrimp	6.3	9.7	**0.0**	**13.7**	0.0	6.1	6.9	**0.0**	**13.7**	0.0	0.1
Other bent. inver.	4.6	7.1	**0.0**	**10.0**	6.7	4.5	7.1	**0.0**	**10.0**	9.6	9.4
Large zooplankton	43.1	66.2	**0.0**	**93.7**	11.1	42.0	66.2	**0.0**	**93.7**	60.6	16.4
Small zooplankton	46.0	70.7	**0.0**	**100.0**	82.2	44.9	70.7	**0.0**	**100.0**	29.3	73.1
Total	100.0		0.0	217.4	100.0	100.0		0.1	222.4	100.0	100.0
TRN	4					11					

Table 4. Diet compositions of herring used in modelling of the southern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

Southern Gulf	1985–1987					1994–1996				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Small cod										
American plaice										
Flounders										
Small demersals										
Capelin										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	**0.3**	0.5	0.0	0.7	0.3	**0.7**	9.7	0.0	13.7	0.7
Other bent. inver.	6.1	7.1	**0.0**	**10.0**	5.3	**0.0**	2.0	0.0	2.8	0.0
Large zooplankton	41.6	17.5	**26.5**	**51.3**	36.2	26.5	66.2	**0.0**	**93.7**	40.8
Small zooplankton	52.0	24.1	**38.7**	**72.8**	58.3	72.8	70.7	**0.0**	**100.0**	58.5
Total	100.0		65.3	134.7	100.0	100.0		0.0	210.2	100.0
TRN	4					4				

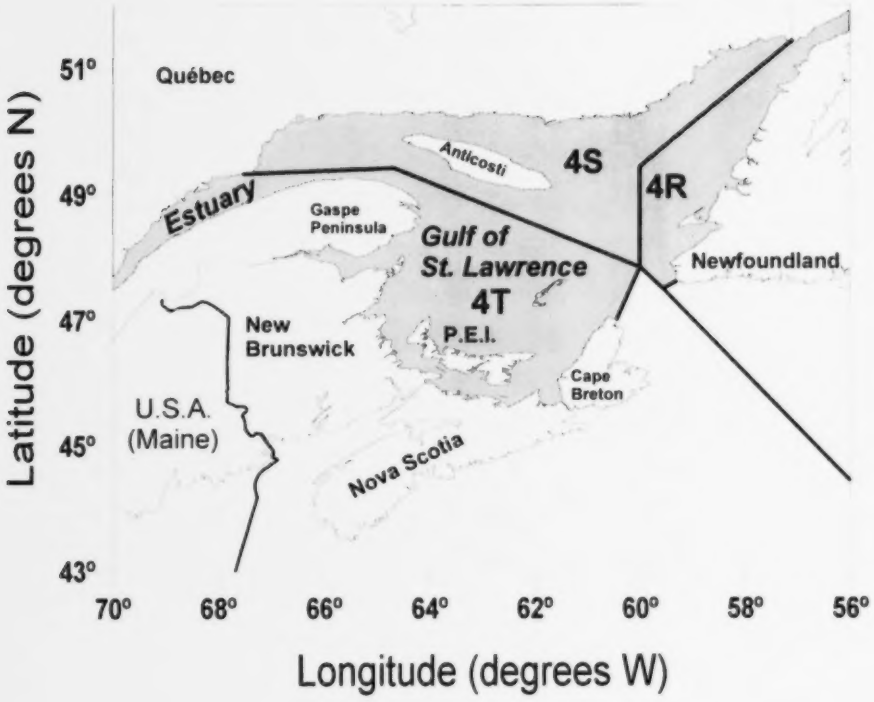

Figure 1. Study area: northern (NAFO divisions 4RS) and southern (NAFO division 4T) Gulf of St. Lawrence. The St. Lawrence Estuary was not included in this study.

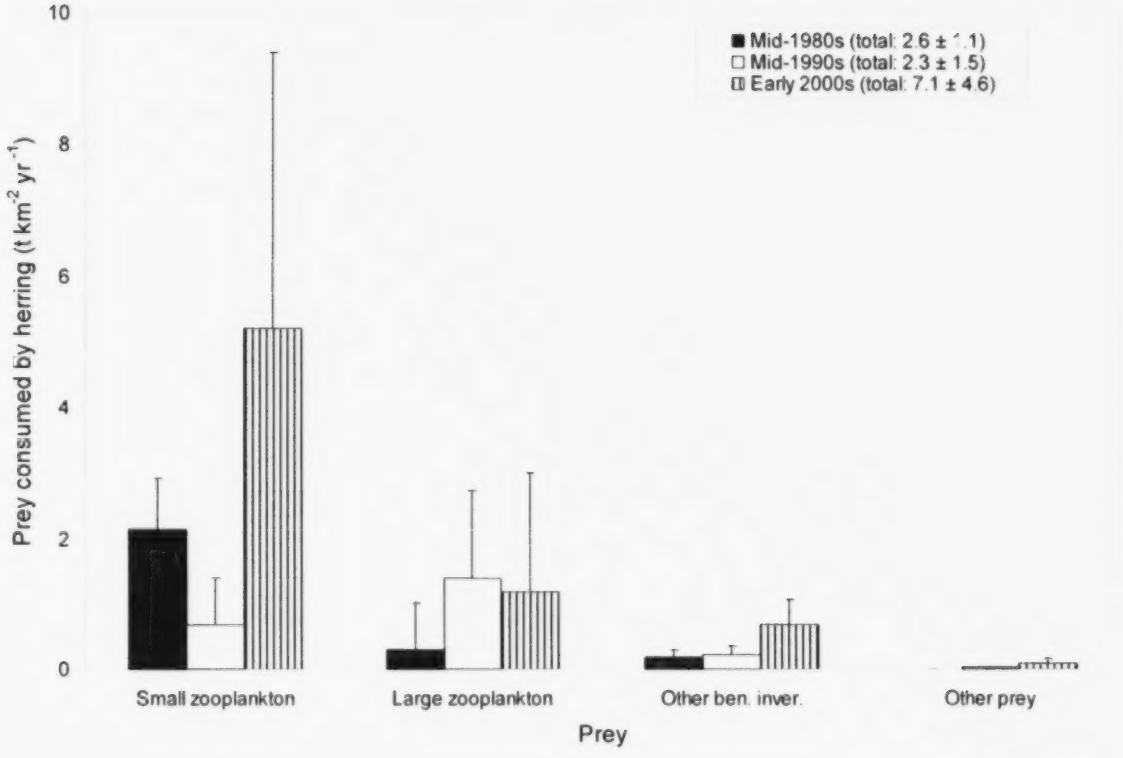

Figure 2. Prey consumed by herring estimated for each time period in the northern Gulf. Total herring consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

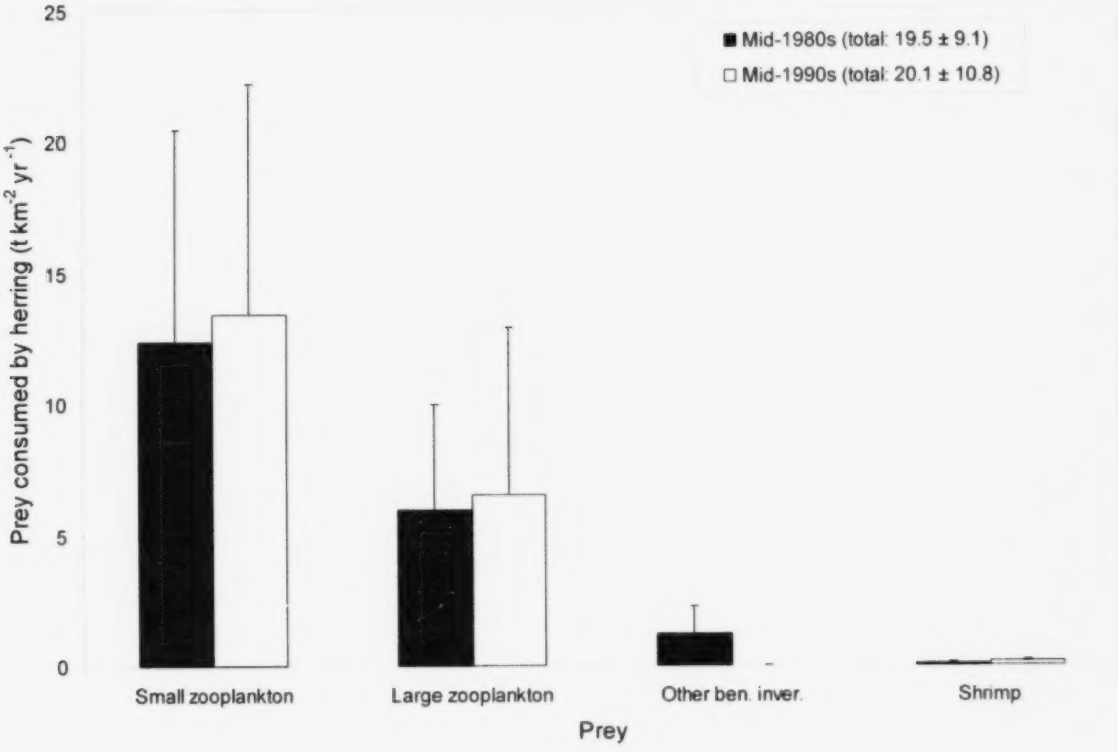

Figure 3. Prey consumed by herring estimated for each time period in the southern Gulf. Total herring consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

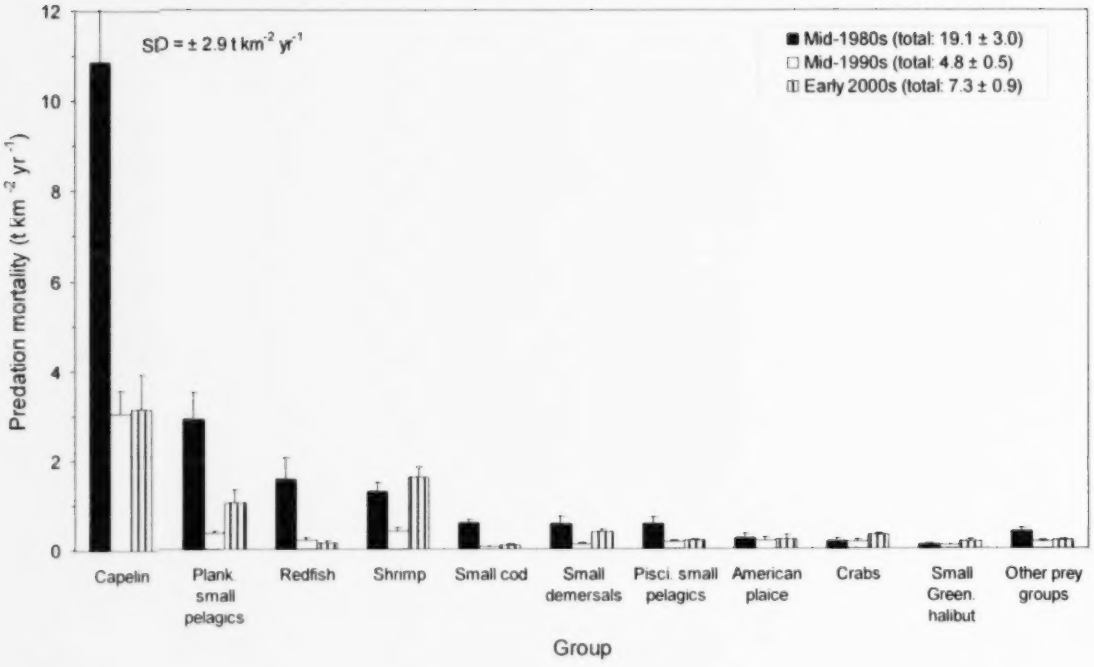

Figure 4. Main vertebrate and crustacean prey consumed in the northern Gulf estimated for each time period. Bars show mean values and SD.

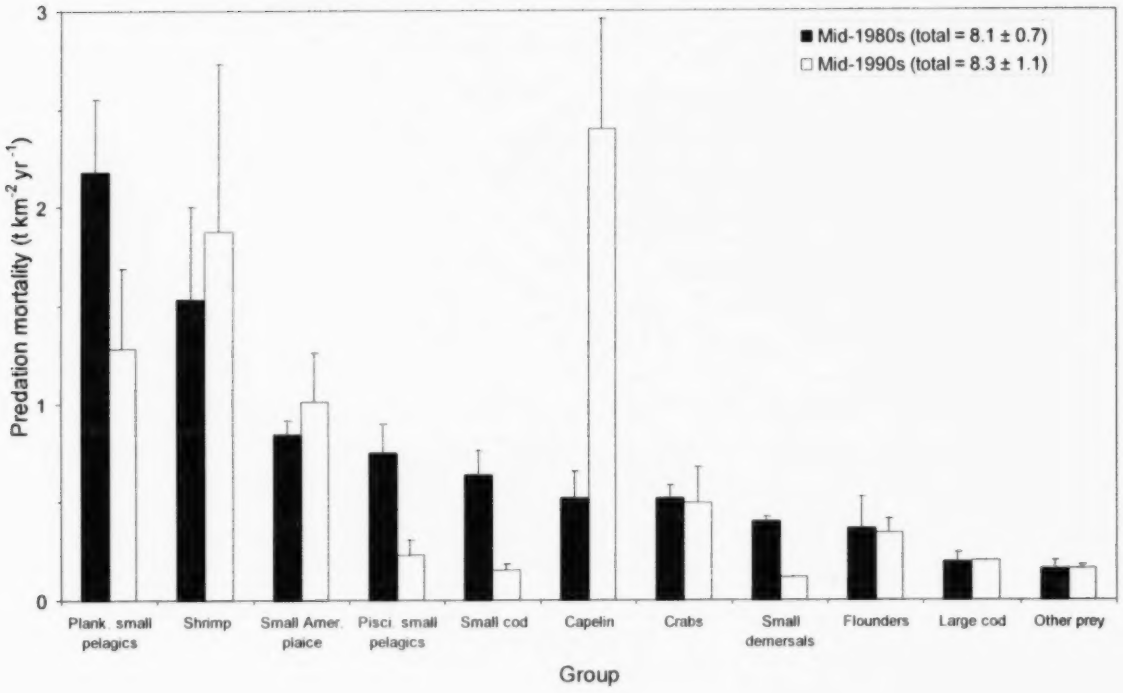

Figure 5. Main vertebrate and crustacean prey consumed in the southern Gulf estimated for each time period. Bars show mean values and SD.

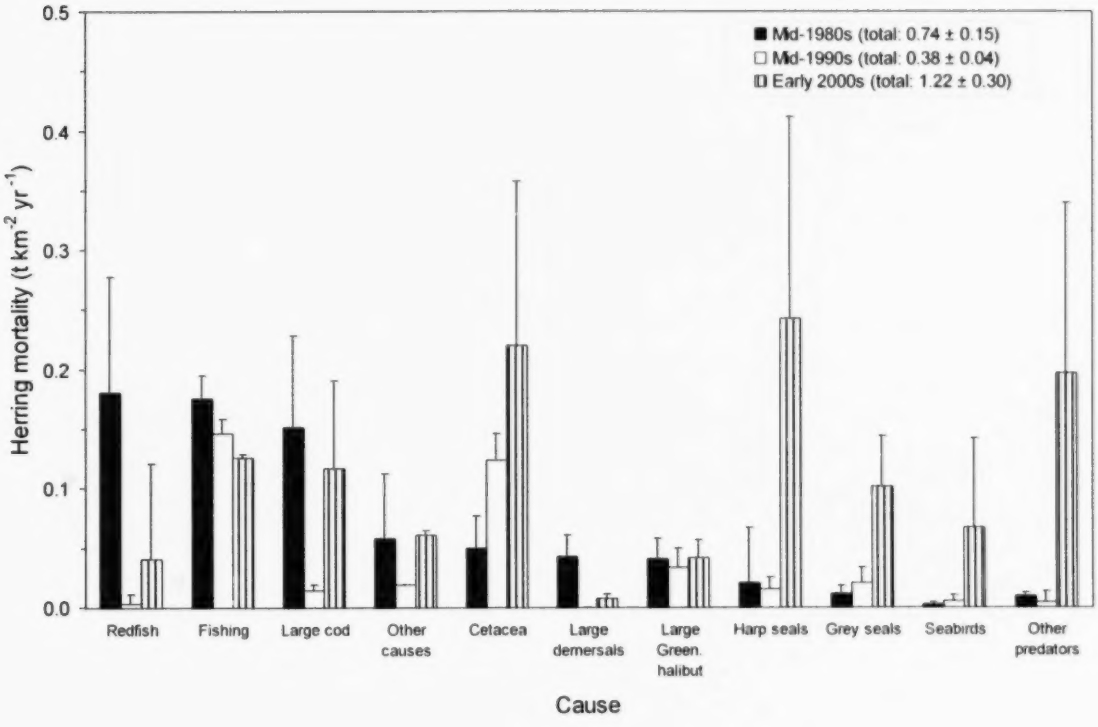

Figure 6. Main causes of herring mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the northern Gulf. Bars show mean values and SD.

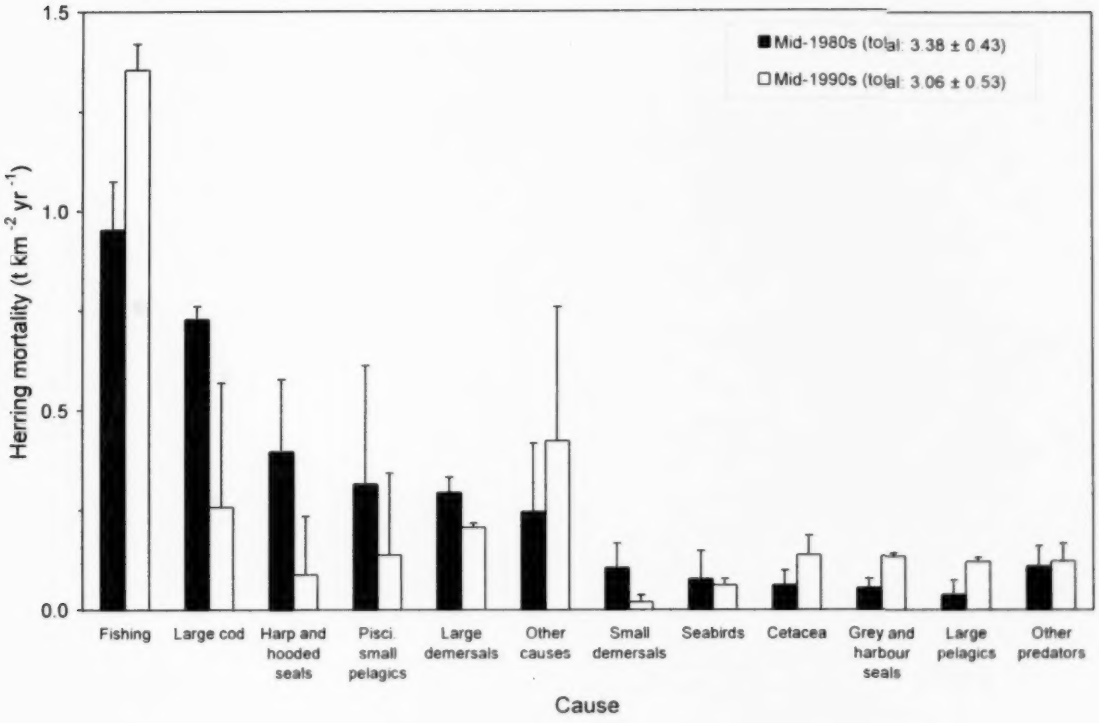

Figure 7. Main causes of herring mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the southern Gulf. Bars show mean values and SD.